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ON THE ORIGIN OF THE SUBTERRANEAN FAUNA OF NORTH AMERICA.

BY ALPHEUS S. PACKARD.[1]

Having, in my essay on the Cave Fauna of this continent, attempted to bring together as many facts as possible bearing on this subject, in now addressing the members of this Congress on the topic assigned me, it will be well to first give a *résumé* of the general subject and then to call attention to the additional facts and conclusions relating to this interesting topic.

In that work I took the view that the cave fauna of this country, and presumably of the world in general, was formed of emigrants or colonists from the surrounding regions of the upper world. I may be permitted to give an extract from what I published in 1888, in order to call attention to the scope of the inquiry.

"The conditions of existence in caverns, subterraneous streams and deep wells, are so marked and unlike those which environ the great majority of organisms, that their effects on the animals which have been able to adapt themselves to such conditions at once arrest the attention of the observer. To such facts as are afforded by cave-life, as well as parasitism, the philosophic biologist naturally first turns for the basis of

[1] Read at the meeting of the Zoological Congress of the World's Auxiliary Congress of the Columbian Exposition, Chicago, 1894.

his inductions and deductions as to the use and disuse of organs in inducing their atrophy. It is comparatively easy to trace the effects of absence of light on animals belonging to genera, families, or orders in which eyes are normally almost universally present. As we have seen in the list already given of non-cavernicolous animals, the eyes are wanting from causes of the same nature as have induced their absence in true cave animals. No animal or series of generations of animals, wholly or in part, loses the organs of vision unless there is a physical, appreciable cause for it. While we may never be able to satisfactorily explain the loss of eyes in certain deep-sea animals from our inability to personally penetrate to the abysses of the sea, we can explore caves at all times of day and night, of winter and summer; we can study the egg-laying habits of the animals, and their embryonic development; we can readily understand how the caves were colonized from the animals living in their vicinity; we can nicely estimate the nature of their food, and its source and amount, as compared with that accessible to out-of-door animals; we can estimate with some approach to exactitude the length of time which has elapsed since the caves were abandoned by the subterranean streams which formed them and became fitted for the abode of animal life. The caves in Southern Europe have been explored by more numerous observers than those of this country, and the European cave fauna is richer than the American, but the conditions of European cave-life and the effects of absence of light and the geological age of the cave fauna are a nearly exact parallel with those presented in the pages of my memoir. Moreover, the cave-life of New Zealand and the forms there living in subterranean passages and in wells, show that animal life in that region of the earth has been affected in the same manner. The facts seem to point to the origin of the cave forms from the species now constituting a portion of the present Plistocene fauna; hence they are of very recent origin."

The advances in our knowledge of cave-life made since 1886 and 1887, may be referred to under the following heads:

I. The fauna of caves, subterranean waters and wells, and their origin, investigated by H. Garman, Herrerao, Girard, Bolivar, Cope and Stejneger.

II. New facts regarding blind non-cavernicolous or lucifugous forms, comprising the anatomical and physiological investigations of Eigenmann, Hess, Kadyi, Schlampf, Ritter, and others.

III. Embryological observations on the conditions of the eyes in the young or in the embryos, tending to prove the origin of blind forms from normal eyed ancestors, by Teller and by Eigenmann.

IV. Theoretical discussions, by Weismann, Herbert Spencer, Lankester, and others.

I. It is very desirable to make a thorough survey of the animal life living at present in the region around the entrances of caves, in order to ascertain the eyed forms from which the blind ones may have originated. This Professor Garman has begun to do for the cave-region of Kentucky. In his article in "Science," on the origin of the cave-fauna of Kentucky," while he remarks that "the geological evidence is all that could be desired for proof of a recent origin of the caves themselves," he dissents "from the conclusions which have been drawn from this proof, as to the recent origin of the blind animals," claiming that animals which burrow in the soil everywhere show a tendency to loss of the organs of vision," and that "the originals of the cave species of Kentucky were probably already adjusted to a life in the earth before the caves were formed," and adds, "I cannot believe that there has been anything more than a gradual assembling in the caves of animals adapted to a life in such channels. In this view of the matter the transformation of eyed into eyeless species appears to have been much less sudden and recent than has been supposed." He illustrates his point by the "definite example of the blind crustacean, *Caecidotaea* (Asellus) *stygia*, which, though first discovered in caves, is also widely distributed in the upper Mississippi Valley, occurring as far east as Pennsylvania. "It is, throughout its range, a creature of underground streams, and is nowhere more common than on the prairies of Illinois

(the last place in the country in which one would expect to find a cave), where it may be collected literally by the hundreds at the mouths of the tile-drains and in springs. In Kentucky also it is not more abundant in the cave region than elsewhere, being very frequently common under rocks in springs and in streams flowing from them, even during its breeding season. It is only natural that such a crustacean should have found itself at home in Mammoth Cave when this cave was ready for its reception."

"I scarcely see what grounds there are for supposing that the present cave species are older than the remaining Quaternary fauna. All the blind and eyeless or partially eyed species must, in the beginning, have descended from normally-eyed forms, while the loss of vision or the disappearance of eyes, even where the rudiments of eyes remain, may, in some cases, have been comparatively sudden (by which we mean after several generations, or less, say, than a hundred), or in others have required hundreds of generations. In some cases, as in that of *Caecidotaea*, forms living in subterranean streams or under stones or buried in the soil, may have become already modified before being carried, or before migrating into the caves."

Mr. Garman then refers to the blind fishes, giving some new facts regarding their distribution. Finally he writes of the distribution of the blind beetles of the genus Anophthalmus, and gives an interesting account of a new species (*A. hornii*) discovered in fissures in the Trenton limestone of Lexington, Ky. This is an interesting example of the way in which a species living in conditions intermediate between an out-of-door life under stones or in the soil and in caves, becomes gradually adapted to a cavernicolous existence. The author also states his belief "that there appears to have been, after the Champlain period, a migration towards Mammoth Cave of cave insects from the south and east, when the continent had not been so greatly affected by changes of level as was the Mississippi Valley. Mr. Garman also sees nothing to indicate that cave animals have ever been more completely isolated than they are now, a view with which we agree. This does not conflict with the general

view we have expressed that isolation is an important factor in the evolution of the fauna of caves, of subterranean waters, and of other dark situations.

Other additions to our subterranean fauna have been noticed by Mr. S. Garman, who finds in the caves of southwestern Missouri, in which are subterranean streams, besides *Typhlichthys subterraneus* Girard a new species of blind crayfish (*Cambarus setosus* Faxon); what "seems" to be *Ceuthophilus sloanii* Pack. and *Asellus hoppiae* Garman, "from Day's Cave, in mud under stones;" the latter form seems to be a genuine, eyed *Asellus*, and allied to an undetermined species represented on Pl. IV, fig. of our memoir, collected from a brook near Lancaster, Ky. The six other species of invertebrates mentioned belong to common out-of-door species, including a dragon-fly, a Dineutes, and a Hydrotrechus, and need not have been mentioned in connection with cave insects, as multitudes of insects naturally occur at or near the mouth of caves.

Here might be mentioned the interesting discovery by Mr. Nathan Banks of the common Phalangid of Wyandotte Cave, *Scotolemon flavescens* Cope, "under stones on the Virginia shore of the Potomac near Washington, D. C.," which, he says, "does not differ from cave specimens."[2]

A blind Salamander has also been discovered in this country by Mr. Stejneger. In the Rock House Cave, Missouri, on the walls, about 600 feet from the entrance, occurred a blind salamander (*Typhlotriton spelaeus*), forming a new genus and species of the family Desmognathidae. In the single adult captured the eyes are said to be "concealed under the continuous skin of the head." A larva was found, but, strangely enough, the condition of the eyes in the young is not referred to.

Passing out of our territory into Mexico, Professor Alfonso L. Herrera describes the results of his researches on the fauna of Cacahuamilpa Grotto, in Mexico. The new or more interesting forms are the following:

[2] The Phalangida Mecostethi of the United States. Trans. Amer. Ent. Soc., XX, 149–152. June, 1893.

INSECTS.

Choleva cacahuamilpensis (Ch. spelaea Bilmk.).
Tachys cacahuamilpensis (Bembidium unistriatum Bilmk.).
Ornix cacahuamilpensis (Ornix impressipenella Bilmk.).
Pholeomyia cacahuamilpensis Herrera.
Phalangopsis cacahuamilpensis Herrera (Ph. annulata Bilmk.).
Lepisma cacahuamilpensis Herrera (L. anophthalma Bilmk.).

ARACHNIDA.

Phrynus cacahuamilpensis Herrera (Ph. mexicanus Bilmk.).
Drassus cacahuamilpensis Herrera (D. pallidipalpis Bilmk.).
Nesticus cacahuamilpensis Herrera (Pholcus cordatus Bilmk.).

MYRIOPODA.

Scutigera cacahuamilpensis Herrera.

CRUSTACEA.

Armadillo cacahuamilpensis Bilmk.

I have received from Professor Herrera an eyeless Asellid crustacean taken from a well at Montery, Leon, Mexico. It shows no traces of eyes, and apparently belongs to a new genus, the species also being undescribed.

II. NEW FACTS REGARDING BLIND, NON-CAVERNICOLOUS, OR LUCIFUGOUS FORMS.

Although not a cave-dweller, the blind goby of the Californian coast lives in similar conditions and tells the same story as the blind Proteus of the cave of Adelsberg or the blind salamander of the Missouri Cave, of the loss of eyesight by disease. The blind goby (*Typhlogobius californiensis* Steindachner) occurs abundantly at Point Loma, San Diego, under rocks between tide-marks in holes made by "crabs" (more properly, shrimps). As Professor C. H. Eigenmann tells us, in his paper on the "Fishes of San Diego:" "It has been found nowhere else about San Diego, but has been taken at Ensenada. Its

habitat is, as far as known, quite limited. In its pink color and general appearance it much resembles the blind fishes inhabiting the caves of southern Indiana. Its peculiarities are doubtless due to its habits. The entire bay region is inhabited by a carideoid crustacean which burrows in the mud. It, like the blind fish, is pink in color. Its holes in the bay are frequented by Cleavelandia, etc., while at the base of Point Loma, where the waves sometimes dash with great force, the blind fish is its associate. . . . . In the bay the gobies habitually live out of the holes, into which they descend only when they are frightened, while at Point Loma this species never leaves its subterranean abode, and to this fact we must attribute its present condition.

"How long these fishes have lived after their present fashion it would be hard to conjecture. The period which would produce such decided structural changes can not be a brief one. The scales have entirely disappeared, the color has been reduced, the spinous dorsal has been greatly reduced; not only have the eyes become stunted, but the whole frontal region of the skull, and the optic nerves have been profoundly changed.

"The skin, and especially that of the head, has become highly sensitized. The skin of the snout is variously folded and puckered and well-supplied with nerves; the nares are situated at the end of a fleshy protuberance which projects well forward, just over the mouth. At the chin are various short tentacles, and a row of papillae, which very probably bear sensory hairs similar to those represented in Figs. 15 and 16 (Plate XXIII), extends along each ramus of the lower jaw, and along the margin of the lower limb of the preopercle. The eye is, however, the part most seriously affected. In the young, Fig. 7, it is quite evident, and is apparently functional. Objects thrust in front of them are always perceived, but the field of vision is quite limited. With age, the skin over the eye thickens, and the eyes are scarcely evident externally. As far as I could determine, they do not see at this time, and certainly detect their food chiefly, if not altogether, by the sense of touch. A hungry individual will swim over meats, fish or a mussel, etc., intended for its food without perceiving it by

sight or smell, but as soon as the food comes in contact with any portion of the skin, especially of the head region, the sluggish movements are instantly transformed, and a stroke of the fins brings the mouth immediately in position for operations."

Here, again, it may be observed that this blind fish is probably not older than the beginning of the Plistocene period, since we know that the coast of California has been rising since the Pliocene epoch, and therefore the coast lines have materially changed since the end of the Tertiary.

For a very full and elaborate account of the degenerate eyes of this blind fish we are indebted to Mr. W. E. Ritter, in an essay published during the present year. Besides the eyes he treats histologically of the integumentary sense papillae, and of the integument of this animal, giving a summary of his results on pp. 96 and 97, which we in part reproduce.

1. In the smallest examples of the blind goby studied, the eyes, though very small, are distinctly visible even in preserved specimens, the lens being plainly seen. In the largest specimens, on the other hand, they are so deeply buried in the tissue as to appear even in the living animals as mere black specks, while in preserved ones they are, in many cases, wholly invisible.

2. As is the case with rudimentary organs in general, the eye is subject to great individual variation in size, form, and degree of differentiation.

3. The only parts of the normal teleostean eye of which no traces have been found are the *argentea*, the *lamina suprachoroidea*, the *processus falciformis*, the cones of the retina, the vitreous body proper, the lens capsule, and, in one specimen, the lens itself.

4. In the parts present the rudimentary condition of the organ is seen in the very slight development of the choroid; in the fact that the choroid gland is composed entirely of pigment; in the fact that the iris, though of fully the normal thickness, is almost entirely composed of pigment; with great proportional thickness of the pigment layer of the retina and the entire absence in it of anything excepting pigment; in the minute size of the optic nerve, and finally in the small size of the *motores oculi.*

5. The surest evidences of actual degeneration are found, first, in the greatly increased quantity of pigment, and secondly, in the presence of pigment in regions where none is found in the normal eye, as in the hyaloid membrane.

6. On comparing the eyes of all blind vertebrates that have been most carefully studied, all may, in a general way, be said to be passing along the same degenerative path.

7. The eyes of blind vertebrates furnish very little evidence on the question whether structures in undergoing actual degeneration in ontogeny follow the reverse order of their phylogeny.

Ritter also states that from the works of European authors it is possible to make a detailed comparison of the eyes of Typhlogobius with those of *Proteus anguinus* and of the European mole, which he proceeds to do. On the whole, the eye of Proteus is more rudimentary than that of either Typhlogobius or Talpa, the lens being absent in the cave Amphibians. All authors, except Semper, are agreed that the optic nerve is present in both Proteus and Talpa, but Ritter finds no account of it ever having, in either of these animals, a pigment-sheath in its passage through the retina, such as occurs in Typhlogobius.

III. Embryological Observations on the Condition of the Eyes in the Embryo or in the Young, proving the Origin of the blind or eyeless Forms from normally-eyed Ancestors.

No complete observations have, so far as we are aware, been made on the embryology of cave animals, nor on that of eyeless non-cavernicolous forms, except in the few cases which we proceed to mention. In our essay on the Cave Fauna of North America (p. 139), we record the fact that in the young of the blind crayfish (*Orconectes pellucidus*), the eyes of the young are perceptibly larger in proportion to the rest of the body than in the adult, the young specimen observed being about half an inch in length. Previously to this, Dr. Tellkampf, in 1844, remarked that "the eyes are rudimentary in the adults, but are larger in the young." Mr. S. Garman

states, regarding the blind Cambarus of the Missouri Cave: "Very young specimens of *C. setosus* correspond better with the adults of *C. bartonii;* their eyes are more prominent in these stages, and appear to lack but the pigment." In the blind cave-shrimp (Troglocaris) of Austria, Dr. Joseph discovered that the embryo is provided in the egg with eyes.

In this connection should be recalled the observations of Semper in his Animal Life (p. 80, 81) on *Pinnotheres holothuriae,* which lives in the "water-lungs" of Holothurians, where, of course, there is an absence of light. The zoëa of this form has large, "well-developed eyes of the typical character. Even when they enter the animal, they still preserve these eyes; but as they grow they gradually become blind or half-blind, the brow grows forward over the eyes, and finally covers them so completely that, in the oldest individuals, not the slightest trace of them, or of the pigment, is to be seen through the thick skin, while, at the same time, the eyes seem to undergo a more or less extensive retrogressive metamorphosis."

In this connection may be mentioned the case of the burrowing blind shrimp (*Callianassa stimpsonii*) which has been found by Professor H. C. Bumpus, at Wood's Holl, Mass., living in holes at a depth of between one and two feet. He has kindly given me a specimen of the shrimp, which is blind, with reduced eyes, smaller in proportion to the body than those of the blind crayfish. He has also obtained the eggs, and has found that the embryos are provided with distinct, black, pigmented eyes, which can be seen through the egg-shell.

Recently, Zeller has studied the embryology of the Proteus of Adelsberg Cave, and has confirmed the statement of Michahelles, who, in 1831, discovered that the eyes of this animal are more distinct in the young and somewhat larger than in the adult. We quote and translate from Zeller's acccount:

"The development of the eyes is very remarkable; they are immediately perceived and present themselves as small, but entirely black and clearly drawn circular points with a slit which is very narrow and yet, at the same time, well-defined, and which penetrates from the lower circumference out to the middle.

"Indeed, one can hardly doubt that this astonishing development of the eye has been accomplished by the influence of light as has also the pigmentation of the skin, the reddish-white ground color of which appears thickly studded with very small brownish-gray points mixed with detached white ones, over the upper surface of the head and over the back down over the sides of the yellowish abdomen. Even on the edge of the fins (Flossensaum) the pigment is found. On the other hand there is a whitish spot over the snout as is likewise the case in the adult creatures which have been colored by the light. Both the under surface of the head and the entire abdomen are shown free from pigment like the limbs. . . . .

"I cannot specify very exactly as to when the pigmentation of the skin begins, but, in any case, it is very early and often earlier that the first beginning of the eyes can be discovered. The latter occurs toward the end of the twelfth week, at which time a thin, light gray line, which still appears overgrown, may be perceived, forming a half circle open underneath. Then while this line subsequently becomes clearer and darker and its ends grow further under and towards each other, there also takes place simultaneously a progression of the pigment larger towards the middle point, and the circle finally seems closed and filled up to the narrow slit mentioned above, which proceeds from the lower circumference and penetrates to the middle of the eye." (p. 570, 571.)

But the most striking discovery bearing on this subject is that of the condition of the eyes in the embryo and young compared with the adult of the blind goby of San Diego.

In his essay on the Fishes of San Diego, Professor Eigenmann briefly refers to and gives four figures (Pl. XXIV) of the embryo of Typhlogobius, Mr. C. L. Bragg having been fortunate enough to discover the egg in the summer of 1891. "The eyes develop normally, and those of Fig. 4 differ in no way from the eyes of other fish embryos." In this case, then, we have the simplest and clearest possible proof of the descent of this blind fish from individuals with eyes as perfect as those of its congeners.

We have been permitted by the Director of the United States National Museum to reproduce Professor Eigenmann's

excellent figures on the embryo, which tell the story of degeneration of the eye from simple disease of the organ, the species being exposed to conditions of life strikingly different from those of its family living in the same bay.

Before the discovery of the eggs, the youngest individual ever seen is represented in Pl. XXIII, fig. 7, its eyes being though small, yet distinct, and "apparently functional."

From these data it is obvious that future embryological study on cave animals will farther demonstrate their origin from ancestors with normal eyes.

IV. Theoretical Results bearing on the Theory of Descent, and more especially on the Neolamarckian Phase of the Theory, including the Doctrine of the Transmission of acquired Characters.

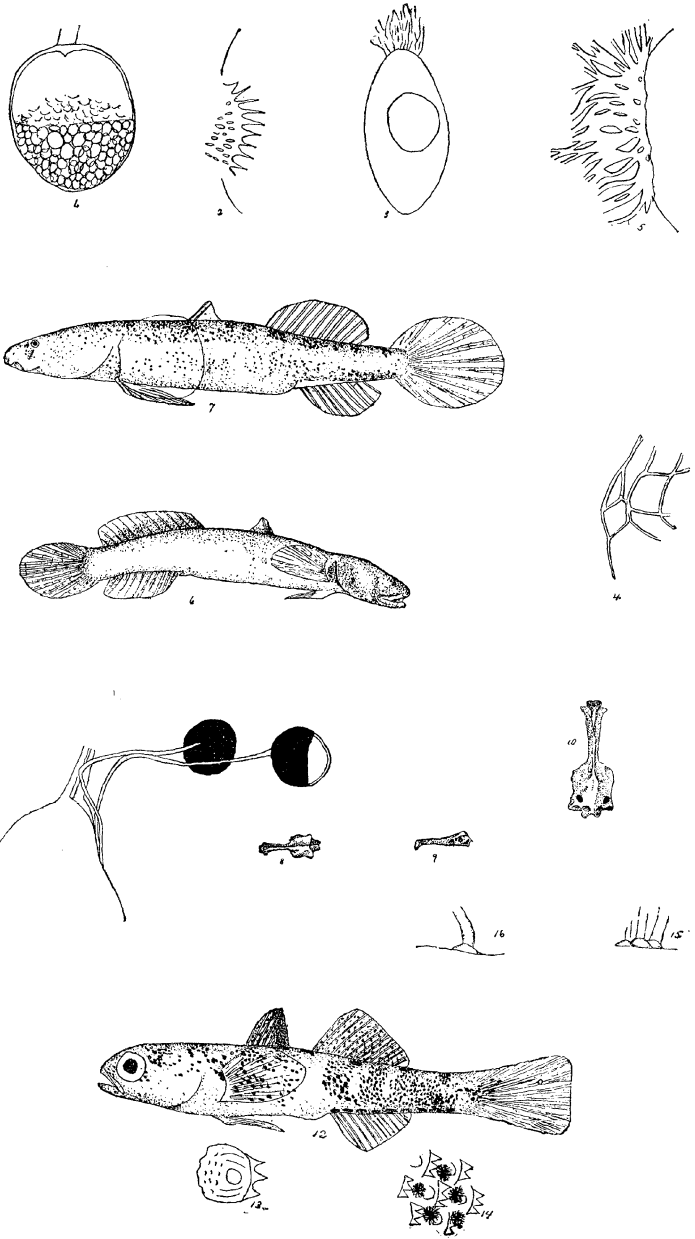
It is evident that the cases just cited afford the strongest possible proof of the theory of evolution in general, and do not militate against the truth of the Neolamarckian phase of the theory, which holds that by a change of environment, inducing disuse of the eyes, such variations, especially atrophy of a part or whole of the eyes and optic nerves and ganglia have become established, so as to result in the origin of new species and even new genera.

In the case of the blind goby, the burrowing Callianassa, the blind shrimp of Adelsberg Cave, and, in fact, nearly, if not quite all the blind forms now known, it is easy to see that the causes of variation are quite direct and appreciable, and that we do not need to invoke the principle of natural selection. And this is the view of Darwin himself.[3]

Besides the factors of change of environment and of disuse, the influence of the isolation of these forms from their out-of-doors' allies should not be overlooked. Take the case of the blind goby of San Diego Bay, or the Callianassa of Buzzard's Bay. Living in habitats remote from their congeners, obvi-

[3] In our work on the Cave Fauna of North America we have discussed the bearing of the facts of cave-life on the Darwinian and Lamarckian phases of evolution and have attempted to show that natural selection is inoperative in such cases as these, quoting Darwin's own words when referring to the loss of eyes in such animals: "I attribute their loss wholly to disuse." (p. 137–143).

PLATE XXIII.



Typhlogobius, Etc.

ously as soon as their ancestors took up a burrowing mode of life, they were prevented from crossing with others of their species, and, probably, when in sporadic cases it did occur, very soon the swamping effects of intercrossing wholly ceased, only those in which the eyes had begun to degenerate interbreeding. After a few generations, therefore, owing to this isolation, the partially blind forms became fixed by heredity and by the very force of circumstances a blind or eyeless generation resulted.

These circumstances are paralled by the results of the intermarriage of deaf-mutes. Professor A. Graham Bell[4] has pointed out the danger of the establishment of a distinct variety of deaf-mutes with a special sign language of their own, since owing to their peculiar social environment and isolation in society there has lately arisen a strong tendency of deaf mutes to intermarry. The result, so far as gathered from a tolerably wide range of facts, shows that this incipient deaf mute strain or variety may have originated in two generations, since it seems probable, as Mr. Bell remarks, "that the oldest deaf mute in the country whose parents were both deaf mutes is now only a little past middle age."

Moreover, the cases we have cited tend to show that the origination of new species and genera of subterranean, as well as deep sea forms and others living in darkness, may have been induced after comparatively few generations. Future observations should be directed to this point. The moment that several individuals became isolated in dark holes or in caves, and more or less confined in such narrow limits, the effects of darkness would at once begin to be experienced, and some degree of adaptation to their changed conditions would immediately begin to operate. The individuals of this generation, i, e., the new comers in the cave, or those gobies which by burrowing in the mud had penetrated out of reach of their

[4] On the formation of a deaf variety of the human race. Memoirs National Academy of Sciences for 1883, Washington, ii, 179–262, 1884. The author points out the means of isolation of deaf mutes through asylums and national, state and city associations for promoting social intercourse, often resulting in intermarriages. He also gives "specimen cases to prove that in many different parts of the country deafness has been transmitted by heredity." (p. 210).

congeners, would doubtless become used to life in darkness. Their offspring of the first generation might or might not suffer some alteration in the visual organs, but doubtless some slight degree of physiological change would result; this might or might not be latent in the next generation, or it might crop out and become manifested in the first generation, or, if not in the first, in the second or third. As soon as the degeneration in the eye-sight began to become fixed by heredity, the process must have gone on rapidly, and, in a few generations, perhaps a dozen or twenty, or fifty, rather than many hundreds or thousands, or "numberless generations," as most writers since Darwin claim.

Now as deaf mutes already appear to breed true to their incipient strain or variety, whether congenitally deaf or rendered so by disease during the lifetime of either or both parents, it seems most probable that animals not at first congenitally blind, might have acquired, after having been carried into, and after living for some months or even years in darkness, the tendency to blindness, and have transmitted to their offspring such first steps in adaptation to their Cimmerian environment. It is difficult for any one, it seems to us, not hidebound by theory to imagine any other mode of procedure.

The steps in the process are these: 1, The change in environment from normal conditions to partial or total darkness; 2, At first a slight degree of adaptation to such change, if the animal survived at all; 3, Becoming gradually habituated to the darkness, compensation for the loss of eyesight would result in the stimulation of the senses of touch and smell; 4, Meanwhile the physiological change from loss of eyesight would react on the physical structure and the eye would begin to degenerate, and very rapidly, after a few generations, the optic nerves in some forms, or the optic lobes and nerves in others, would disappear, the vestiges of the outer structures of the eyes remaining in some forms long after the nervous connections between the eyes and the brain had become effaced; 5, Meanwhile, segregation would prevent intercrossing with newcomers provided with perfect eyes, and consequently would prevent the swamping of the new characters resulting from

disuse; 6, The new variety or species or genus, as the case might be, would become persistent, as long as the conditions of total or partial darkness continued.

Now these factors, so simple, so easily appreciated, that as early as 1802, Lamarck could see their force, though he only cited the case of the mole, for he knew nothing of cave animals—these factors would seem to be adequate for the production of these eyeless forms. These results of disuse seemed adequate to Darwin himself, the founder of the doctrine of natural selection; and yet the extreme Darwinians or Neo-darwinians of the present day push aside or are purblind to these fundamental factors of organic evolution, and insist that the *vera causa* of the evolution of these blind forms is either natural selection or panmixia, and they likewise deny that there is any ground for the operation of the principle of transmission of acquired characters.

Weismann, who has rendered such eminent service to biology, in establishing the principle of heredity on a physical basis, as is well-known, pushes aside all these factors and explains the blindness of cave animals by a negative cause, "panmixia," i. e., the absence of natural selection. In his "Essays on Heredity" (1889) he claims that the small eyes of moles and of other subterranean mammals can be explained by natural selection, and remarks: "I think it is difficult to reconcile the facts of the case with the ordinary theory that the eyes of these animals have simply degenerated through disuse" (p. 86). He assumes that the degeneration of the eye of Proteus "is merely due to the cessation of the conserving influence of natural selection," and, he adds farther on, "this suspension of the preserving influence of natural selection may be termed Panmixia." And he even goes so far as to express the opinion that "that the greater number of those variations which are usually attributed to the direct influence of external conditions of life, are to be attributed to panmixia." He thus substitutes for the positive, tangible factors of change of environment, disuse and isolation, the negative and hypothetical one which he calls "panmixia."

In his discussion on this subject, as well as those of others who have adopted his views, Weismann, and his English translators, do not always give evidence of having carefully read the statements of those who have paid some practical attention to cave animals, Weismann only referring to the cases of the mole and of the Proteus. For instance, he remarks, "If disuse were able to bring about the complete atrophy of an organ, it follows that every trace of it would be effaced (pp. 90 and 292). Now in our "Cave Fauna of North America," published two years before the issue of the English translation of Weismann's essays, we have shown from microscopic sections that in the different species of blind beetles (Anopthalmus) not only is every trace of the optic ganglia and of optic nerves wanting, but also every trace of the eyes themselves. Also in the blind myriopods of Mammoth Cave, *Scoterpes copei*, no traces of the optic ganglia, optic nerves, or of any part of the eyes, including the pigment of the retina or the corneal lenses, were to be discovered. While in the blind crayfish the degenerate eyes are retained, in some individuals of an Asellid (*Caecidotaea stygia*), the eyes may be entirely effaced as well as the optic ganglia and optic nerves. On p. 118 of the memoir referred to there is a summary view of the effects upon the eyes, optic ganglia, and optic nerves, of different Arthropods resulting from living in total darkness.

Again, on p. 87, Weismann makes the following somewhat loose statement: "blind animals always possess very strongly developed organs of touch, hearing and smell." We have laid special emphasis in our essay on compensation by the development of tactile and other organs for the loss of eyesight or of eyes in cave animals, and while Weismann's assertion is true as regards the tactile and olfactory senses, it is curious that, from the direct and repeated observations of Dr. Sloan, which we quote, the blind fish occurring in Wyandotte Cave is, contrary to Wyman's and to Cope's suppositions, not sensitive to sounds.

The blind crayfish of Mammoth Cave, and also the species (*Orconectes hamulatus*) of Nickajack Cave, have, as we have ascertained by anatomical investigation, degenerate ears, so

that the sense of hearing is, with little doubt, nearly, if not quite, obsolete (p. 128).

While, then, Weismann claims that there is a cessation of natural selection in the case of cave animals, another writer, Lankester, in a brief note in *Nature*, asserts that the blindness of cave animals is due to natural selection, remarking: "This instance can be fully explained by natural selection acting on congenital fortuitous variations. Many animals are thus born with distorted or defective eyes, whose parents have not had their eyes submitted to any peculiar conditions. Supposing a number of some species of Arthropod or fish to be swept into a cavern or to be carried from less or greater depths in the sea, those individuals with perfect eyes would follow the glimmer of light and eventually escape to the outer air or to the shallower depths, leaving behind those with imperfect eyes to breed in the dark place. A natural selection would thus be effected. In every succeeding generation (bred in the dark place) this would be the case, and even those with weak but still seeing eyes would, in the course of time, escape, until only a pure race of eyeless or blind animals would be left in the cavern or deep sea."

This explanation seems, however, vague and speculative, as well as inadequate, when we compare the kind of natural selection here invoked with such direct, powerful and readily appreciated factors as partial or total darkness (no plants being able to grow in caves, and only a very scanty fauna); added to the disease of organs whose very existence was originally due to the stimulus of light, and where, were it not for their enforced isolation, the swamping effects of crossing with eyed forms would constantly tend to prevent the permanent existence of blind or eyeless forms. Besides, how can the variations be fortuitous when the overshadowing and all-prevailing influence is darkness, this cause inducing a change primarily in a single organ, and, in a single sense, due to a single cause, urging the variation in a determinate way? Indeed, it may be questioned whether variations are ever "fortuitous" in the sense that they can arise independently of and are not controlled by the ever active forces of nature.

It is apparent that both of the last named writers, who have not themselves had a practical experience in collecting and studying cave animals and their surroundings, nor have carefully read the recent literature on the subject, are overmastered by speculative views, and prefer to make an extremely vague, unscientific and *a priori* speculation, rather than adopt an opinion based on the inductive method.

In refreshing contrast are the views of the veteran English philosopher, Mr. Herbert Spencer, who, like Darwin, fully appreciates the direct bearings of disuse as a fundamental factor, and, with his rare good sense and penetration, recognizes the probability of the active agency of the principle of the transmission of acquired characters in the origin of cave life.

Indeed, in caves, deep holes or burrows, or in dark subterranean streams and wells, to which the blind are restricted, we have conditions very closely parallel to those which obtain in asylums for the deaf and dumb. The array of facts presented by Professor A. Graham Bell and the danger which exists of the formation of a distinct deaf-mute variety of mankind, and the suggestions which he offers as to the most practicable way to arrest the further development of the incipient variety, all afford an interesting and striking parallel to the case of blind animals which are to be found living in caves and similar places.

The cave fauna, as a whole, is composed of individuals, all existing under the same conditions, living in partial or total darkness, and with eyes either defective or absent. Now, how did they come there? We occasionally find, all over the world, creatures with defective sight or imperfectly-developed eyes, but such cases are sporadic, and are not numerous enough in proportion to the normal population to breed together and to multiply. Where, however, individuals with more or less defective eyes should breed with normal mates, any tendency to the transmission of such defects would be wiped out by the swamping effects of crossing, owing to the immense preponderance of normal, vigorous forms with perfect vision. The whole tendency in nature in the upper world of light is to weed out such sporadic, defective forms. But in limestone

regions honeycombed with caves and permeated with subterranean streams, like those in the Mediterranean regions, France, Spain, and Austria, or in those of southern Indiana, Virginia, Kentucky and Missouri—in such regions as these, there exist the conditions favorable to the origination and perpetuity of blind forms. To give an example, eyed geodephagous beetles, such as the species of Trechus, of which there are so many in southern Europe, accustomed to burrowing in the soil under stones, when carried down by various accidents into dark crevices or into caves from which they are unable to extricate themselves, and too hardy and vigorous to succumb to the deadly effects of a life in perpetual darkness, and with, perhaps, already partially lucifugous habits, such forms under these changed conditions survive, breed and multiply, finding just enough food to enable them to make a bare livelihood, and with just enough vigor to propagate their kind. We can easily imagine that in time, and indeed no very long period, the newcomers would soon become adapted to their new surroundings, an environment abnormal both from the absence of light, and from the lack of predaceous forms to devour them; and they would live on, weak, half fed, half blind, forced to make their asylum in such forbidding quarters.

Where are there, in such circumstances as these, any of the conditions which would imply that any struggle for existence or processes of natural or sexual selection in these troglobitic societies are possible? On the contrary, it seems to us that in such unwonted conditions as these, darkness, lack of suitable food, and lack of destructive, carnivorous forms, other than the blind species themselves, we are brought face to face with the more powerful, primary, purely physical agents, which have produced changes chiefly operating in a single direction, i. e., to destroy the vision and to more or less completely abolish the eyes. Here we see exemplified in a typical way the direct action of the Lamarckian factors, viz.: Change of surroundings, coupled with disuse of parts useless in such altered conditions, and then the enforced isolation, especially marked in the cases of the Proteus and of the blind crayfish, etc., which never occur out of caves, however it may be with those species

living in dark wells or subterranean streams, which have a more or less direct connection with the upper world.

As regards the problem of the transmission of acquired characters, it would appear that the case with cave animals is paralled by that of deaf mutes collected together in asylums, and united by various social organizations. It has been shown in a striking way by Mr. Turner, as quoted by Bell, that "before the deaf and dumb were educated, comparatively few of them married." Bell concludes, from an examination of the records of deaf mute asylums in the United States, "that of the deaf mutes who marry at the present time, not less than 80 per cent marry deaf mutes, while of those who married during the early half of the present century the proportion who married deaf mutes was much smaller."

It was also clearly indicated that "a hereditary tendency towards deafness, as indicated by the possession of deaf relatives, is a most important element in determining the production of deaf offspring," and "it may even be a more important element than the mere fact of congenital deafness in one or both of the parents."

It appears, then, that it is the segregation of deaf mutes, inincluding nearly half of the deaf mutes who became deaf from accidental causes, which has led to the apparent increase of this incipient strain or breed of human beings. And the statistics and conclusions given by Mr. Bell appear to almost demonstrate the fact of the transmission of characters acquired during the lifetime of the individual, and that it is difficult to draw the line between this phenomenon and the transmission of congenital characters; the latter being, at present, the more frequent and therefore normal law of heredity, though it was not so in the beginning. For, as Bell, after a careful study of statistics, remarks, "The numbers of the non-congenitally deaf are evidently subject to great and sudden fluctuations on account of the epidemical diseases which cause deafness, whereas, the growth of the congenitally-deaf population seems to be much more regular."

Premising that heredity does not, at the best, always unerringly act, that its results are sometimes uncertain, even where

those with congenital variations breed together or intermarry, it is also to be taken for granted that it may, at times, be impossible to draw the line between the transmission of congenital and of acquired characters.

When a number, few or many, of normal, seeing animals enter a totally dark cave or stream, some may become blind sooner than others; in others there may be developed only a tendency to blindness, the eye itself being imperceptibly modified by disuse, while a certain percentage may possess the tendency plus a slight physical defect, either functional or organic, in the eyes, especially in the optic nerves and ganglia. The result of the union of such individuals and of adaptation to their stygian life would be broods of young, some with vision unimpaired, others with a tendency to blindness, while in others there would be noticed the first steps in degeneration of nervous power and of nervous tissue. Even in a succeeding brood, or in a third brood, we might have a few individuals which were born blind or partly so, and were compelled to feel their way about the cave, while the far more numerous members of the colony would only exhibit a tendency to the disuse of their eyes, attempting to see their way rather than to feel it. Thus, after a few, or only several generations, the society of troglodytes, vertebrate and invertebrate, might be compared to a newly-established asylum of deaf mutes or to an asylum for the blind, if they interbred in the same proportions.

At first, then, the number of cases of those not congenitally blind, but which, after living for most of their life time in darkness and becoming so modified that they could dispense with the use of their eyes, *pari passu* becoming more and more dependent on the exercise of their tactile organs—at first, such individuals as these would greatly preponderate.

So all the while the process of adaptation going on, the antennae and other tactile organs increasing in length and in the delicacy of structure of their olfactory and tactile structures, while the eyes were meanwhile diminishing in strength of vision and their nervous force giving out; after a few generations, (perhaps, judging by what we know of the sudden production of deaf mutes in human societies, only two or

three,) the number of congenitally blind would increase, and, eventually, they would, in their turn, preponderate in numbers.

It is also possible that the longevity of cave animals, owing to the absence of ordinary enemies and of casualties, such as occur in the upper world, even though the supply of food were greatly restricted, would be much greater than in epigaean regions. If this be so, then there is a more favorable opportunity for the development and fixation of the myopic condition in subterranean situations.

It thus appears that while the heredity of acquired characters was, in the beginning, the general rule, as soon as the congenitally blind preponderated, the heredity of congenital characters became the normal state of things, the inhabitants being all blind, and for generations breeding true to their specific and generic characters.

On the other hand if the conditions should be changed, and the cave become opened to the light, then we should expect a gradual reversion to their eyed ancestors. This process would, of course, be due to causes exactly opposite to those producing the blind form, i. e., the presence of light, etc. In such a case, neither natural selection nor panmixia would be the factors, although some one might give a high-sounding, "scientific" name to the supposed process. And this shows how inoperative can be natural selection or panmixia as true working causes of the transformation of species, compared with the operation of the fundamental factors of organic evolution postulated by the Neolamarckian.

List of Essays and Articles Relating to Blind or Cave Animals Published Since 1887.[5]

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[5] This list is supplementary to that published in my essay on the Cave Fauna of North America Memoirs of the National Academy of Sciences, 1889, and includes some titles omitted in that bibliography, many of which are copied from Ritter's work.

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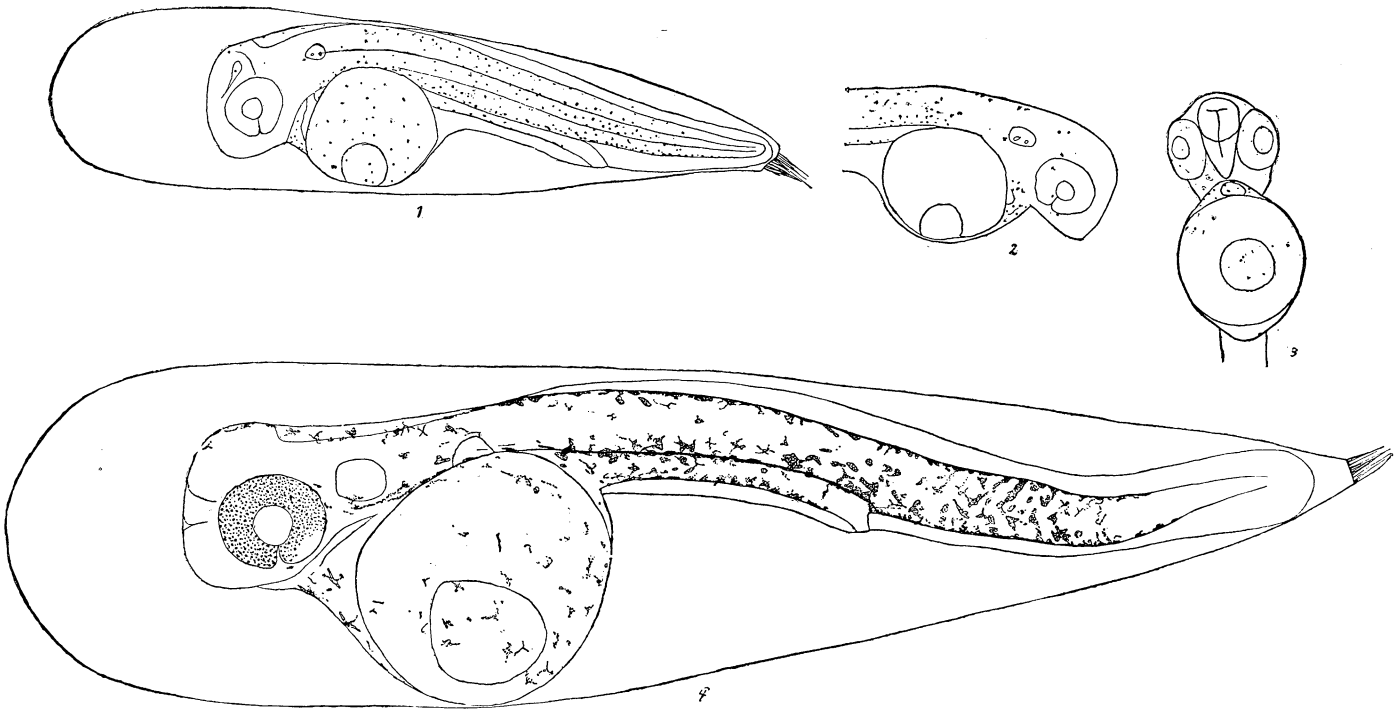
PLATE XXIV.



Typhlogobius.